ASSESSING A MACROALGAL FOUNDATION SPECIES:

COMMUNITY VARIATION WITH SHIFTING ALGAL ASSEMBLAGES

By

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Abstract

Foundation species provide critical food and habitat to their associated communities. Consequently, they are disproportionately important in shaping community structure, promoting greater biodiversity and increased species abundance. In the Aleutian archipelago, once extensive kelp forests are now relatively rare and highly fragmented. This is due to unregulated urchin grazing shifting the majority of nearshore rocky-reefs from kelp forests to either urchin barrens or "transition forests" – kelp forests devoid of understory algae. The algal communities within kelp forests, transition forests, and urchin barrens represent a stepwise loss in fleshy algal guilds, a regression from a full algal community, to having only canopy kelp, to areas largely denuded of all fleshy algae. This stepwise loss of algal guilds was used to test the designation of the resident canopy-forming kelp, *Eualaria fistulosa*, as a foundation species—a species that has strong, positive effects on communities where it occurs. Therefore, I assessed the impact that *E. fistulosa*'s occurrence had on faunal community structure (in terms of species diversity, abundance and biomass, and percent bottom cover)and invertebrate size-structure. This study found that the presence of *E. fistulosa* does not correspond to strong differences in invertebrate size-structure or faunal community structure. However, in kelp forests where *E. fistulosa* exists in tandem with a variety of subcanopy macroalgae, faunal communities are more species rich, have significantly different community structures with notably higher abundance, biomass, and percent cover of filter feeding taxa, and support sea urchin populations containing significantly higher proportions of larger individuals. Consequently, this study stresses the context dependent role of foundation species and suggests their strong, positive effects on associated communities may change with perturbations to ecosystems. To that end, this study suggests that we may need to reconsider the designation of *E. fistulosa* as a foundation species following the extensive fragmentation and range restriction that has occurred throughout much of the Aleutian Archipelago.

Table of Contents

Page

List of Figures

Page

List of Tables

Page

List of Appendices

Page

Introduction

Where foundation species occur, they have strong, positive effects on communities by stabilizing local environments, acting as critical food resources, and creating biogenic structure that provides critical habitat for other species (Dayton 1972; Graham et al. 2013). Many biological communities are hierarchically organized by facilitation from foundation species (*i.e.,* every community member, except for one foundation species, is dependent on a member in the next lower trophic level), with competition and predation acting as secondary factors that further shape the community (Altieri et al. 2007). Consequently, foundation species are disproportionality important to the structure and functioning of their associated community by increasing diversity, survivorship, and species abundance (Dayton 1972; Stachowicz 2001; Bruno et al. 2003). Much of our understanding of how foundation species affect communities comes from marine ecosystems where dominant, structure-forming species, or species guilds, facilitate the associated community. Examples include coral reefs, intertidal mussel beds, mangrove forests, seagrass meadows, and kelp forests (Jones et al. 1994; Alongi 2002; Graham 2004; Peterson et al. 2004; Gaylord et al. 2011).

Although foundation species are easily defined, identifying the role of foundation species within ecosystems can be difficult. One hurdle is that many biogenic habitats (*e.g.,* coral reefs, mussel beds, mangrove forests, seagrass meadows, kelp forests) are structured by multiple foundation species that are often lumped into a single functional guild whose members are assumed to play redundant or additive roles (Bruno and Bertness 2001). However, individual foundation species may exhibit differences in their structural and functional morphology that differentiate their effect on communities (Bruno and Bertness 2001) and facilitation by multiple foundation species may be synergistic (Jones et al. 1997). For example, coral reefs are composed of many coral species whose various growth forms (encrusting, laminar, columnar, foliaceous, massive, or branching) operate together to create complex biogenic coral reef structures that promote species diversity (Knowlton and Jackson 2001). In another example, mixed stands of kelp in Australia occur more often and harbor more diverse invertebrate assemblages than monospecific stands (Goodsell et al. 2004).

Whether a particular taxon qualifies as a foundation species can be context dependent, as one species may function differently across systems (Graham et al. 2013). For example, within soft sediment habitats, clams can provide hard substrate critical for sessile invertebrate attachment, thereby functioning as foundation species (Gribben et al. 2009). However, in mixed or hard sediment habitats, clams are not necessary as a substrate for sessile invertebrates and would not be considered a foundation species for their ability to provide this critical habitat. Determining how foundation species interact and how they affect the associated community under different conditions is important for understanding the relative importance of species for ecosystem functioning and for informing conservation and management efforts.

In temperate rocky-reef marine ecosystems, kelps produce subtidal "forests" that can modify light, nutrient, hydrodynamic and larval recruitment patterns within their boundaries, and provide food and shelter for a diverse fauna (Steneck et al. 2002; Graham 2004; Arkema et al. 2017). Consequently, many of the dominant kelp species in kelp forest communities are considered foundation species (Graham et al. 2013) (Figure 1). Within kelp forests, non-kelp fleshy macroalgae are also common and can increase the complexity of a forest. As such, within forests, kelp and other associated fleshy macroalgae can be broadly categorized by their heights into three morphological groups, or guilds: canopy kelp are the largest and produce floating canopies; understory algae are smaller but are held above the benthos by their ridged stipes; and prostrate algae are the smallest, covering the benthos with their stipes, and include the non-kelp species (Dayton 1985). For the purposes of this study, understory kelp and prostrate algae will collectively be called "subcanopy" algae. One example of a foundation kelp species is the giant kelp, *Macrocystis pyrifera*. This perennial species has been shown to slow currents within kelp forest boundaries (Jackson 1977), enhance the recruitment of fish and invertebrate species (Carr

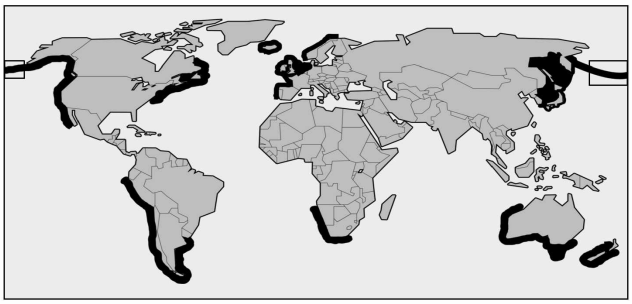

Figure 1: Global map showing shaded coastal areas where the kelps *Macrocystis pyrifera, Nereocystis luetkeana, Laminaria* spp., or *Ecklonia* spp. act as foundation species (modified from Graham et al. 2013). In the boxed areas along the central to western Aleutian Archipelago the canopy kelp *Eualaria fistulosa* forms monospecific kelp canopies and is thought to be a foundation species.

1994), and increase species richness (Graham 2004). Similarly, the subcanopy kelps *Agarum fimbriatum* and *Saccharina groenlandica* of the San Juan Archipelago (Washington State, USA) were found to reduce flow and turbulent mixing within their boundaries, increasing sediment accumulation and suspension feeders' growth rates (Eckman and Duggins 1991).

While kelp, particularly canopy kelps, can act as foundation species (Mann 1973; Field et al. 1977; Drew 1983; Kirkman 1984; Larkum 1986; Graham et al. 2013), their role is context dependent. For example, in the Northeast Atlantic, *Laminaria hyperborea* is an important foundation species, providing much of the habitat and energy for communities where it occurs (Christie et al. 2009; Araújo et al. 2016); however, in California, a closely related species, *Laminaria farlowii*, likely does not act as a foundation species. There, *L. farlowii* co-inhabits rocky reefs with *Macrocystis pyrifera* and is thought to have a small effect on community structure relative to *M. pyrifera*. Consequently, *L. farlowii* is not thought to be a foundation species in those communities (Graham et al. 2013). Relative to its lower latitude counterparts, little is known about the high-latitude canopy kelp *Eualaria fistulosa* (hereafter *Eualaria)* in terms of primary production rate or how it influences the associated community (Graham et al. 2013; but see Reisewitz et al. 2006; Schuster and Konar 2014; Konar et al. 2015); however, *Eualaria* is widely believed to act as foundation species where it occurs (Estes and Palmisano 1974; Estes et al. 1978; Estes and Duggins 1995; Graham et al. 2013).

Natural communities are often assumed to exist in a stable state that fluctuates around an average structure, and where changing conditions drive gradual changes to that structure (Scheffer et al. 2001); however, large, rapid shifts in community structure can, and do occur through strong top-down pressure via trophic cascades. In trophic cascades, reciprocal predator-prey interactions across multiple food-web links can impact the structure and productivity of the entire community (Pace et al. 1999; Terborgh and Estes 2006). Further, when a trophic cascade impacts a foundation species, the community effect tends to be particularly strong (Ellison et al. 2005). In addition to significantly altering community structure, changes from trophic cascades can shift communities to alternative "stable habitats" (Filbee-Dexter and Scheibling 2014) that can persist long after the initial driver of the community shift has reversed (Lauzon-Guay et al. 2009; Ling et al. 2009).

On temperate rocky reefs, kelp forests and sea urchin barrens are considered alternate stable habitats (Filbee-Dexter and Scheibling 2014). Urchin barrens are characterized by the dominance of sea urchins and encrusting coralline algae, and the near complete removal of kelp and other fleshy algae (Filbee-Dexter and Scheibling 2014). Urchin barrens generally exhibit lower primary productivity and structural complexity than kelp forests (Simenstad et al. 1978; Graham 2004; Filbee-Dexter and Scheibling 2014). Sea urchins mediate the habitat-shift between kelp forests and urchin barrens through grazing on kelp and associated algae (Lawrence 1975; Ling et al. 2014). Various biotic and abiotic processes are capable of controlling sea urchin populations and precipitating the shift from kelp forests to urchin barrens, or visa-versa. In eastern Tasmania, for example, ocean warming has extended the range of the long-spined sea urchin (*Centrostephanus rodgersii*). This range expansion, combined with heavy fishing of the region's primary urchin predators (*e.g.*, spiny lobster *Jasus edwardsii)* has resulted in many of the region's kelp forests shifting to urchin barrens (Ling et al. 2009). Similarly, the large kelp forests of central Norway appear to be maintained by higher diversities and populations of sea urchin predators such as crabs, wolfish, and cod (Stadniczeñko et al. 2015). On the rocky reefs of the Atlantic Coast of Nova Scotia, sea urchin populations are controlled by disease mortality (Lauzon-Guay et al. 2009). There, periodic warm water intrusion introduces the amoeba *Paramoeba invadens,* which has been associated with mass urchin mortality and the subsequent establishment of kelp forests. In the Northeast Pacific, predation by sea otters (*Enhydra lutris*) tend to regulate urchin populations, thereby initiating a trophic cascade and determining the structure of the dominant rocky reef habitat (Estes and Duggins 1995; Watson and Estes 2011).

Sea otters are a well-known predator capable of exerting top-down control on sea urchins in the Aleutian Archipelago (Estes and Palmisano 1974). Through sea urchin predation, sea otters maintain kelp forests by keeping sea urchin abundance low or causing them to flee or have cryptic behavior, all of which reduces herbivory on fleshy macroalgae (Estes and Palmisano 1974; Watson and Estes 2011; Spyksma et al. 2017). Consequently, where sea otters are abundant, sea urchin abundance is low and fleshy macroalgae are abundant; whereas where sea otters are sparse (less than six sea otters per km of

coastline) (Estes et al. 2010) or absent, sea urchins are abundant and remove fleshy macroalgae through overgrazing (Estes et al. 1978).

After being hunted to near extinction in the Aleutians, northern sea otters (*Enhydra lutris keyoni*) began to recover once commercial hunting ceased in 1911 (Doroff et al. 2003). Northern sea otter populations increased through the 1980s but then declined drastically during the 1990s, resulting in a 75% decrease between 1965 and 2000 (Doroff et al. 2003). This population decline has been attributed to predation on sea otters by killer whales *(Orcinus orca*) (Estes et al. 1998). Today, northern sea otters are listed as threatened under the Endangered Species Act with no evidence of recovery (Muto et al. 2017). Further, the remaining sea otter populations have shifted from broadly using all available nearshore habitats to utilizing only those nearshore habitats expected to provide the greatest refuge from killer whale predation (Estes et al. 2010; Stewart et al. 2014). Consequently, sea urchin densities have increased substantially throughout much of the Aleutian Islands and the associated grazing pressure has largely denuded most Aleutian kelp forests (Estes et al. 1998).

Despite the widespread establishment of urchin barrens, some remnant kelp forests persist throughout the Aleutian Archipelago (Konar et al. 2014). Kelp forests in this region are composed primarily of the canopy kelp *Eualaria*; subcanopy kelps from the genera *Agarum, Laminaria*, *Thalassiophyllum*, and *Saccharina*; as well as other subcanopy red (Rhodophyta), green (Chlorophyta), and brown (Desmarestiales*)* algal species (Konar 2000a) (Figure 2). Additionally, a habitat occurs in the region that likely represents a transitional state between kelp forests and urchin barrens (or visa-versa). In these "transition forests" the substrate is denuded of subcanopy algae, but *Eualaria* persists (Schuster and Konar 2014) (Figure 2). These kelp forests and transition forest habitats appear to be

Figure 2: The three dominate nearshore rocky-reef habitats of the Aleutian Archipelago: kelp forests (left) that have the canopy kelp *Eualaria fistulosa* and understory algae present; transition forests (center) have *E. fistulosa* present but lack a subcanopy algal community; and urchin barrens (right) lack all fleshy algae.

maintained by an interaction between sea urchins and fleshy macroalgae, whereby water motion induces macroalgae to "sweep" the nearby substrate, dislodging sea urchins, and precluding grazing (Konar 2000b). As a result, three distinct nearshore rocky-reef habita now exist (kelp forests, transition forests, and urchin barrens) across the region where kelp forests once predominated. Further, these habitats exist in close proximity to one another (often abutting one another but, if not, typically <2km apart) throughout the majority of the Archipelago. These habitats offer a unique opportunity to examine how Aleutian nearshore rocky-reef community structure changes with variation in algal guilds and investigate the role of *Eualaria* as a foundation species.

In addition to the potential impact on community composition and diversity, variation in algal guilds may also impact the size structure of associated organisms. Growth rates of marine invertebrates are physiologically less constrained than most vertebrates or terrestrial invertebrates and highly dependent on food conditions (Sebens 1987). Body size can also be mediated by nutritional condition, with animals experiencing food scarcity often having smaller asymptotic size than those under similar physical conditions with abundant food (Sebens 1987). For example, increased food quantity and quality positively impact growth rates of sea urchins (Lemire and Himmelman 1996; Meidel and Scheibling 1999) while low-energy content encrusting coralline algae (Paine and Vadas 1969) diets support little to no sea urchin growth (Lemire and Himmelman 1996). Thus, if food quantity and quality differ among habitats (*e.g.*, between kelp forests and urchin barrens), then the average body sizes of macroinvertebrate species are likely larger in habitats with higher algal productivity.

This study used the Aleutian Archipelago's nearshore rocky reefs as a natural experiment to examine how variation in foundation species and algal guild composition impacts associated community composition and size structure of rocky reef associated organisms. To achieve this aim, I tested the following hypotheses. The first hypothesis is that sites designated *a priori* as kelp forests and transition forests would have more abundant *Eualaria* than urchin barrens, and kelp forests would have more abundant subcanopy algae than transition forests and urchin barrens. The second hypothesis is that habitats with abundant *Eualaria* would have associated epibenthic faunal communities with higher diversity, greater abundance/biomass of species, and significantly different

primary bottom cover due to *Eualaria's* role as a foundation species. The final hypothesis to be tested is that size-structures of several hard-bodied invertebrate taxa would have a higher proportion of large bodied individuals in habitats with greater *Eualaria* biomass.

Methods

1 Study sites

Nine islands spanning ~1230 km in the Aleutian Archipelago, from Samalga Pass to Agattu Strait, were sampled during two research cruises aboard the *RV Oceanus* in July 2016 and June 2017 (Figure 3). At each island, rocky reef sites were scouted for acceptable depth range (6-8 m), visually assessed from the surface, and given an *a priori* habitat designation of kelp forest, transition forest, or urchin barren. Kelp forests were identified as those sites having canopy kelp and subcanopy algae present, transition forests contained canopy kelp but subcanopy algae were largely absent, and urchin barrens lacked nearly all canopy and subcanopy algae. Two sites belonging to each of the three *a priori* habitats were sampled per island using scuba, for a total of six sampling sites per island. Depending on sites' location and accessibility, sites were separated by tens of meters to several kilometers at each island.

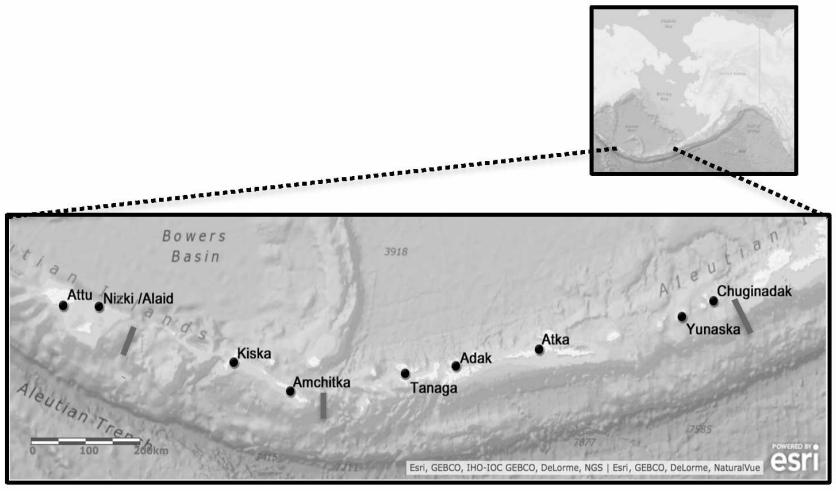

Figure 3: Map of study area showing the islands sampled across the Aleutian Archipelago and major oceanographic features. Coordinates (in decimal degrees, latitude/longitude) for approximate sampling location: Attu: 52.92°, 173.20°; Nizki & Alaid: 52.74°, 174.00°; Kiska: 51.97°, 177.58°; Amchitka: 51.41°, 179.28°; Tanaga: 51.81°, -177.94°; Adak: 51.87°, -176.66°; Atka: 52.10°, -174.69°; Yunaska: 52.66°, -170.74°; and Chuginadak: 52.84°, -169.75°.

2 Sampling methods

To assess community structure at each site, I used three methods. First, to quantify the epibenthic community, ten 0.25 m^2 quadrats were haphazardly placed within each site

and within these quadrats, percent cover was visually estimated for the following categories: bare substrate, the prostrate green alga *Codium*, suspension feeders, encrusting coralline algae, and *Clathromorphum* spp. The sampling differentiated between *Clathromorphum* spp. and other encrusting coralline genera because this could easily be done in the field. *Clathromorphum* spp. can be distinguished from other encrusting coralline genera as they form extensive, pavement-like deposits that can be greater than 0.5 m thick (Lebednik 1976), whereas other encrusting coralline algae (*e.g.*, *Lithothanmion* spp.) form thin (1-5 mm) crusts (O'Clair and Lindstrom 2000). Following visual estimation, all epibenthic organisms occurring within quadrats, except those strongly adhered to the substrate (*e.g.*, barnacles, encrusting coralline algae, etc.), were scraped from the substrate and placed in fine mesh collection bags for shipboard processing. Lastly, three 10 m x 2 m swaths were placed haphazardly at each site. Within each swath, *Eualaria* stipes were counted, midwater and demersal fishes visually quantified by trained divers, and all conspicuous, sparsely distributed large mobile invertebrates were collected in fine mesh bags for shipboard processing. This included sea stars, crab, and large gastropods etc., with densities assumed to be less than 1 per 2.5 m^2 (the total area covered by the above quadrats). Once onboard, all collected organisms were identified to the lowest possible taxonomic level, counted if the taxon has discrete individuals, and weighed using hanging spring scales to determine biomass to the nearest .005 kg. Ambiguous or difficult to identify individuals were preserved in 10% formalin (for invertebrates) or pressed (for algae) for later identification.

3 Statistical analyses

First, habitats were tested to ensure that populations of those taxa used to assign sites to their *a priori* habitat, did indeed differ among habitat. *Eualaria*, subcanopy algae, and sea urchins were each tested independently using two-way, crossed permutational multivariate analyses of variance (PERMANOVA) treating habitat as a fixed factor crossed with sites nested within islands. In subsequent community structure analyses, I excluded data from these taxa in order to focus on the associated faunal communities.

To test for difference in habitats' diversity, three diversity measures were

calculated: Margalef's index of species richness ($d = (S-1)/\log N$)), Pielou's index of species evenness ($J' = H'/\log S$), and average taxonomic distinctness ($\Delta^+ = [\sum\sum_{i<j} \omega_{ij} x_i x_j\ ] / [\sum\sum_{i<j} x_i x_j\ ]$) (Pielou 1966; Shannon 1948; Warwick and Clarke 1995). Margalef's index was included because it incorporates the total number of individuals (N) and therefore attempts to adjust for the fact that within samples with more individuals more species tend to be found. Pielou's index was used as it measures equitability, i.e., how communities compare to a hypothetical community where all taxa are equally abundant. Finally, taxonomic distinctness, a measure of the average taxonomic breadth of samples, was included as a diversity measure as it may be a more sensitive index of community perturbation than measures based on richness or evenness (Warwick and Clarke 1995). To test for differences among habitats one-way analyses of variance (ANOVA) testing for habitat were run for each diversity measure.

Prior to multivariate analyses, community abundance and biomass data were standardized to m^2 and pooled across quadrat and swath collections. All subsequent analytical steps were performed on both abundance and biomass data independently. If a taxon was collected using both collection methods (and therefore represented in both datasets), only data from that method where the taxon was represented in the greater number of sites was used. To down-weight contributions of quantitatively dominate species, all data were fourth root transformed prior to Bray-Curtis similarity matrix calculations (Clarke and Gorley 2015). Next, a two-way crossed PERMANOVA, treating habitat as a fixed factor that was crossed with sites nested within islands, was used to test for differences in community structure among habitats. I included island to account for variation in community composition among islands when assessing community differences among habitat types. Subsequently, for those comparisons that yielded significant differences between habitats, similarity percentages (SIMPER) analyses were run to identify the taxa contributing most to dissimilarities between habitats. Nonmetric multidimensional scaling (nMDS) ordinations were used to visually display dissimilarities in community composition among habitats. Comparative tests on similarity matrices (RELATE routines) were used to test for correlation between Bray Curtis similarity matricides from the biomass of various algae or algal assemblages against the faunal

biomass matrix. This was done to determine which algal guild or taxa had the greatest correlation with overall faunal community structure. The algae used in RELATE routines were the full algal community, all subcanopy algae, all fleshy red algae, *Eualaria, Laminaira* spp., or *Agarum* spp., the latter two being two prominent subcanopy kelp taxa.

The final metric I used for community structure comparisons among habitats were percent cover data. These data were square root transformed, then a Euclidian distance similarity matrix was calculated. A PERMANOVA was employed as above to test for difference between habitats. A SIMPER routine was run to identify the percent cover categories contributing most to dissimilarities among habitats. Dissimilarities among habitats were visualized with a metric multidimensional scaling (mMDS) ordination.

To test the hypothesis that habitats with more *Eualaria* biomass would have a higher proportion of large invertebrates, size-frequency analyses were conducted. Only four taxa for which size data were collected displayed a broad spread in their distribution among habitats and through the study region (*i.e.*, occurred in each of the three habitats in at least four islands). These taxa were sea urchins (*Strongylocentrotus spp.),* the sea stars *Leptasterias camtschatica* and *Henricia lineata,* and the limpet *Lottia scutum*. Multivariate analyses were conducted to test for significant difference in taxon's size-structures among habitats. I used this method because it is a permutational test that incorporates all data points as opposed to other tests that use the largest difference between two cumulative data points. First for analyses, a Euclidian distance similarity matrix was calculated for each taxon's size-frequency matrix (where size was the independent variable, and count on individuals the dependent). Then, analysis of similarity (ANOSIM) routines were run on each similarity matrix-treating habitat as the fixed factor and sites nested within islands as random factors. Additionally, RELATE routines were used to test for correlations between each taxon's size frequency matrix and the Bray-Curtis similarity matrix based on the biomass from either *Eualaria,* subcanopy algae, or entire fleshy algal community (*i.e., Eualaria* plus subcanopy algae). This was done to determine which algal guild (or guild combination) showed the greatest correlation with each taxa's size distributions.

Results

1 Testing a priori habitat designations

Eualaria abundance and biomass did not show significant differences between kelp forests and transition forests (Table 1). However, both kelp forests and transition forests displayed significantly more *Eualaria* abundance and biomass than in urchin barrens (Table 1, Figure 4). Subcanopy algal community abundance and biomass were significantly different and higher in kelp forests than in the other two habitats (Table 1, Figure 4) with subcanopy algae contributing 6.09 ± 2.95 kg/ m^2 to *Eualaria's* 2.54 ± 1.07 kg / m^2 ($\bar{x} \pm S.E.$). Subcanopy algal communities did not differ between transition forests and urchin barrens (Table 1). Sea urchin (*Strongylocentrotus* spp.) abundance and biomass were significantly different and lower in kelp forests than in the other two habitats (Table 1, Figure 4). However, sea urchin abundance and biomass did not differ between transition forests and urchin barrens (Figure 4). These results confirm that initial site surveys were able to appropriately classify sites into their *a priori* habitats.

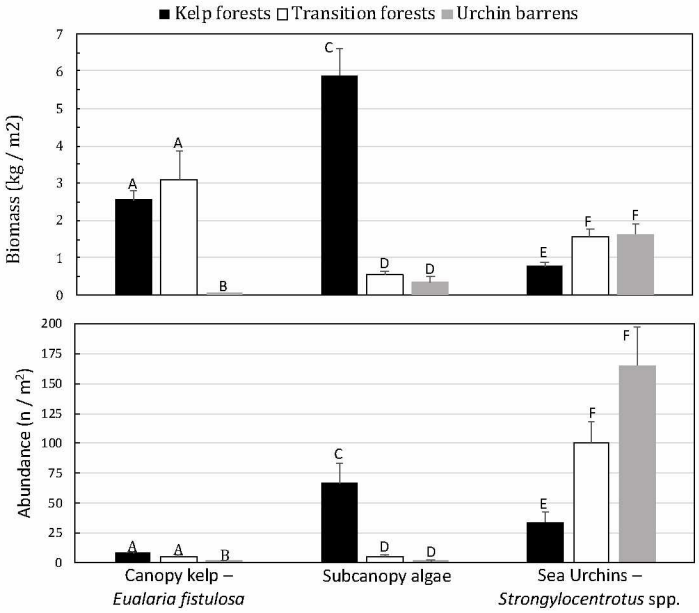

Figure 4: Bar charts of average biomass (top) and abundance (bottom) values (± standard error, S.E.) among habitats for taxa used to classify sites into their *a priori* habitats. Different letters represent significantly different populations among habitats within each taxa as determined by PERMANOVA analyses.

Table 1: Permutational analysis of variance (PERMANOVA) results testing taxa used to visually classify sites to *a priori* habitats.

A priori taxa	Data set	Habitats	t	P (perm)
Canopy kelp	Abundance	Kelp forests, transition forests	1.6897	0.06
Eualaria fistulosa		Kelp forests, Urchin barrens	10.667	0.001
		Transition forests, Urchin barrens	7.9676	0.001
	Biomass	Kelp forests, transition forests	1.2256	0.2747
		Kelp forests, Urchin barrens	23.083	<0.001
		Transition forests, Urchin barrens	10.435	<0.001
Understory algae	Abundance	Kelp forests, transition forests	4.6697	0.001
		Kelp forests, Urchin barrens	6.1179	0.001
		Transition forests, Urchin barrens	1.7644	0.097
	Biomass	Kelp forests, transition forests	4.8329	0.001
		Kelp forests, Urchin barrens	5.3595	0.001
		Transition forests, Urchin barrens	1.9355	0.066
Sea urchins	Abundance	Kelp forests, transition forests	5.7311	0.001
Strongylocentrotus spp.		Kelp forests, Urchin barrens	6.3166	0.001
		Transition forests, Urchin barrens	2.0518	0.063
	Biomass	Kelp forests, transition forests	2.4787	0.0286
		Kelp forests, Urchin barrens	2.2932	0.0397
		Transition forests, Urchin barrens	0.20618	0.8586

2 *Testing hypotheses that habitats with abundant Eualaria have associated communities with higher diversity, greater abundance and biomass of species, and different primary bottom cover.*

Overall, 237 taxa were identified in this study with 6 ascidians, 12 fish, 43 macroalgae, and 176 invertebrates (Table 2). When analyzing species richness (Margalef's index (d)) from community abundance data, kelp forests exhibited significantly richer communities than either transition forests or urchin barrens ($F(1,34)=0.489$, $p=0.034$; $F(1,34)=6.368$, $p=0.0165$); transition forests and urchin barrens did not show a significant difference ($F(1,34)=0.156$, $p=0.696$). However, no habitats exhibited difference in species richness based on their community biomass (kelp forests to transition forests, $F(1,34)=1.933$, $p=0.173$; kelp forests to urchin barrens, $F(1,34)=2.301$, $p=0.139$; transition forests to urchin barrens, $F(1,34)=0.121$, $p=0.730$) (Table 3, Figure 5). Kelp forests exhibited significantly lower evenness (Pielou's evenness index (J')) based on community abundance) than transition forests ($F(1,34)=6.532$, $p=0.015$); however, neither kelp forests nor transition forests were significantly different from urchin barrens in terms of evenness ($F(1,34)=3.334$, $p=0.077$; $F(1,34)=0.992$, $p=0.326$). However, when analyzing evenness based on community biomass, kelp forests exhibited significantly lower evenness than either transition forests or urchin barrens, while the latter two did not differ ($F(1,34)=7.782$, $p=0.009$; $F(1,34)=13.084$, $p<0.001$; $F(1,34)=1.905$, $p=0.177$).

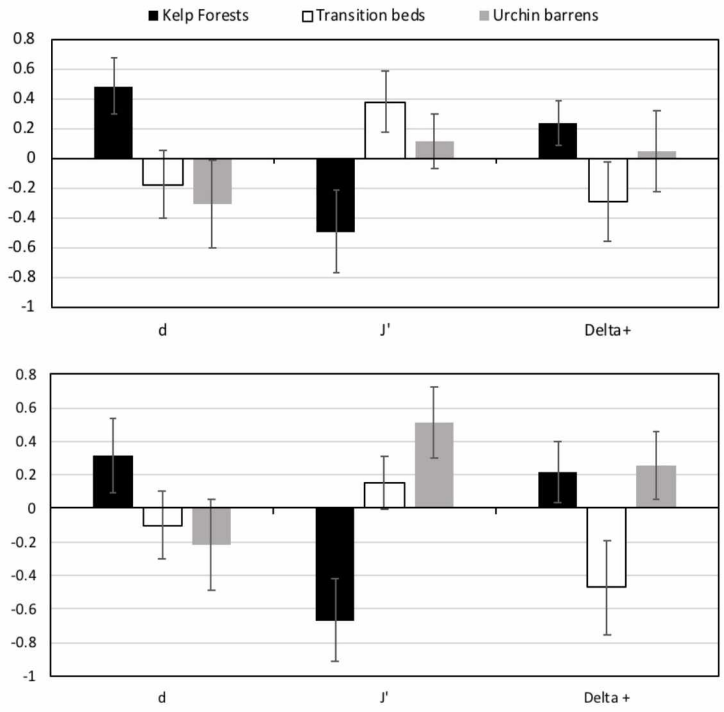

Figure 5: Bar graphs of average, normalized values for species richness (Margalef's index (d)), evenness (Pielou's evenness index (J')), and taxonomic distinctness (Δ+) (± standard error, S.E.) among habitats using abundance data (top) or biomass data (bottom).

Table 2: Contribution to total number of taxa identified in this study by phylum

Phylum	Count
Chordata	18
Chlorophyta	2
Ochrophyta	13
Rhodophyta	28
Annelida	10
Arthropoda	24
Brachiopoda	1
Bryozoa	9
Cnidaria	15
Echinodermata	42
Mollusca	46
Nematoda	1
Nemertea	2
Platyhelmenthes	1
Porifera	22
Sipunclua	2
Total	237

Table 3: Average species richness (Margalef's index (d)), evenness (Pielou's evenness index (J')) and taxonomic distinctness (Δ^+) among habitat and data sets.

Data Set	Phase State	d	J'	Δ^+
Abundance	Kelp forests	7.85 ± 1.42	0.974 ± 0.01	79.25 ± 2.03
	Transition forests	6.65 ± 1.72	0.982 ± 0.01	77.53 ± 3.61
	Urchin barrens	6.41 ± 1.88	0.980 ± 0.01	78.64 ± 3.61
Biomass	Kelp forests	13.16 ± 1.92	0.973 ± 0.01	81.22 ± 1.46
	Transition forests	12.25 ± 1.73	0.980 ± 0.01	79.85 ± 2.32
	Urchin barrens	12 ± 2.35	0.982 ± 0.01	81.29 ± 1.63

Lastly, taxonomic distinctness (Δ^+) did not differ among any habitats' when comparing communities' abundance (kelp forests to transition forests, $F(1,34)=2.912$, $p=0.097$; kelp forests to urchin barrens, $F(1,34)=0.369$, $p=0.548$; transition forests to urchin barrens, $F(1,34)=0.795$, $p=0.379$). However, kelp forests and urchin barrens both exhibited significantly higher taxonomic distinctness compared to transition forests based on community biomass ($F(1,34)=4.211$, $p=0.048$; $F(1,34)=4.393$, $p=0.044$) while kelp forests and urchin barrens exhibited no difference in taxonomic distinctness ($F(1,34)=0.212$, $p=0.884$) (Table 3, Figure 5).

Analyses of community structure based on abundance data showed a significant difference among habitats (PERMANOVA global test, Pseudo-$F=2.292$, $P_{(perm)}<0.001$, SS=12,264). Additionally, kelp forests differed from both transition forests and urchin barrens ($T=1.873$, $P_{(perm)}=0.006$; $T=2.153$, $P_{(perm)}=0.003$), while transition forests and urchin barrens did not differ ($T=1.13$, $P_{(perm)}=0.269$ (Table 4, Figure 6).

SIMPER results indicated that higher densities of the ascidian *Styela rustica* ($\overline{n}$ =1.15/m^2 and 0.08/m^2), the mussel *Musculus niger* ($\overline{n}$ =1.07/m^2 and 0.38/m^2), and the limpet *Tonicella lineata* ($\overline{n}$ =0.83/m^2 and 0.70/m^2) in kelp forests compared to urchin barrens were the taxa that contributed most to the dissimilarity between those habitats (4.64%, 4.20%, and 2.71%, respectively; Table 5, Figure 7).

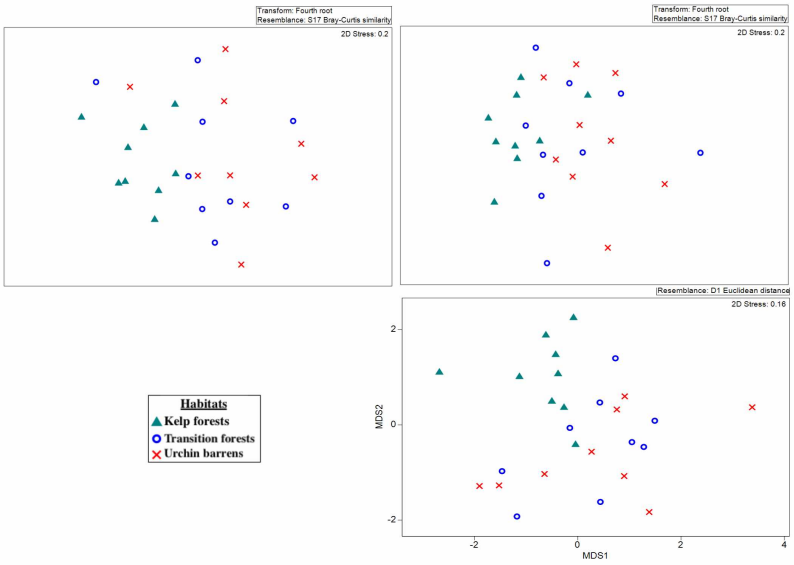

Figure 6: nMDS (top) or mMDS (bottom) plots showing similarities and differences in community structure among habitats for either abundance (top left), biomass (right), or percent cover (bottom). Points represent the different islands' average communities among habitats. Note that in all cases kelp forests shows relatively less overlap with the other habitats, suggesting that the structure of

Table 4: PERMANOVA results testing for differences among habitats' community structure in terms of the associated community abundance, biomass, or percent bottom cover.

Test	Data set	df	SS	MS	Psuedo-F	P(perm)	Unique perms
Global test for Habitat	Abundance	2	12264	6132.1	2.2917	0.00005	91614
	Biomass	2	12328	6164	4.3549	0.00003	570108
	Percent Cover	2	12.089	6.0445	4.7655	0.0007	94921
Pairwise tests among habitats					**T**	**P(perm)**	**Unique perms**
Abundance	Kelp forests, transition forests				1.873	0.006	94623
	Kelp forests, urchin barrens				2.1526	0.0033	94618
	Transition forests, urchin barrens				1.1308	0.2693	94270
Biomass	Kelp forests, transition forests				2.1401	0.0042	656581
	Kelp forests, urchin barrens				2.5349	0.0018	659669
	Transition forests, urchin barrens				1.1767	0.2239	651818
Percent Cover	Kelp forests, transition forests				2.3559	0.0108	95386
	Kelp forests, urchin barrens				2.5938	0.0037	95412
	Transition forests, urchin barrens				1.0124	0.4196	95386

Table 5: Results of SIMPER analyses showing the top three taxa responsible for driving dissimilarity among habitats, for those habitats where a significant difference between their community structure was found.

Data Stream	Taxa	Av. Grp. A Density	Av. Grp. B Density	Av. Diss.	Diss./S.D.	Contrib.%	Cum.%
Abundance	Groups: Kelp forests (A) and Transition forests(B) – Average dissimilarity = 66.15						
	Musculus niger	1.15	0.08	2.85	1.17	4.64	4.64
	Stelya rustica	1.07	0.38	2.58	0.79	4.20	8.84
	Tonicella lineata	0.83	0.70	1.67	1.08	2.71	11.55
	Groups: Kelp forests (A) and Urchin barrens (B) - Average dissimilarity = 66.15						
	Stelya rustica	1.07	0.26	3.29	0.82	4.97	4.79
	Musculus niger	1.15	0.14	3.09	1.24	4.68	9.64
	Leptasterias camtschatica	1.03	0.58	1.80	1.12	2.72	12.36

Biomass	Groups: Kelp forests (A) and Transition forests (B) - Average dissimilarity = 56.49						
	Halichondria sp.	0.66	0.24	2.75	1.66	4.87	4.87
	Acarnus erithacus	0.51	0.22	2.25	1.85	3.99	8.85
	Porifera spp.	0.51	0.18	2.15	1.34	3.81	12.66
	Groups: Kelp forests (A) and Urchin barrens (B) - Average dissimilarity = 60.36						
	Halichondria sp.	0.66	0.12	3.12	1.78	5.32	5.32
	Porifera spp.	0.51	0.24	2.49	1.79	4.12	9.44
	Acarnus erithacus	0.51	0.15	2.48	1.84	4.11	13.55
Percent bottom cover	Groups: Kelp forests (A) and Transition forests (B) - Average dissimilarity = 56.49						
	Suspension feeders	2.22	1.66	2.99	1.77	20.84	20.84
	Codium spp.	0.79	0.98	2.62	1.46	18.30	39.14
	Encrusting coralline algae	2.22	2.48	2.31	1.90	16.11	55.25
	Groups: Kelp forests (A) and Urchin barrens (B) - Average dissimilarity = 56.49						
	Suspension feeders	2.22	1.58	3.18	1.65	20.79	20.79
	Codium spp.	0.79	0.96	2.76	1.22	18.02	38.81
	Clathromorphum spp.	2.22	2.25	2.49	1.65	16.27	55.08

Similar results were found when testing for differences among habitats using biomass data. Overall, habitats differed (PERMANOVA global test, Pseudo-F=4.355, $P_{(perm)}$<0.001, SS=12,328). Again, kelp forests differed in community biomass from both transition forests and urchin barrens, while transition forests and urchin barrens did not differ significantly (T=2.140, $P_{(perm)}$=0.004; T=2.535, $P_{(perm)}$=0.0.002; T=1.177, $P_{(perm)}$=0.223) (Table 4, Figure 6). Several sponge taxa had higher biomass in kelp forests compared to either transition forests or urchin barrens. These were *Halichondria* spp. ($\bar{x}$ =0.66kg/m^2, 0.24kg/m^2, and 0.12 kg/m^2, respectively), *Acarnus erithacus* ($\bar{x}$ =0.51kg/m^2, 0.22kg/m^2, and 0.18 kg/m^2), and *Porifera spp.* ($\bar{x}$ =0.51kg/m^2, 0.22kg/m^2, and 0.24 kg/m^2) and they were most responsible for driving the dissimilarity between kelp forests and transition forests (4.87%, 3.99%, and 3.81%, respectively) and between kelp forests and urchin barrens (5.32%, 4.12%, and 4.11%) (Table 5, Figure 7).

According to RELATE routines, the biomass of the faunal community was significantly correlated to the biomasses of each the entire subcanopy algal community, *Laminaria* spp., and entire fleshy red algae community (R=0.298, p=0.001; R=0.298, p=0.001; R=0.240, p=0.001, respectively) However, faunal biomass was not significantly correlated to biomasses of either *Agarum* spp. nor *Eualaria* were not (R=0.09, p=0.0381; R=1.888, p=0.23) (Table 6).

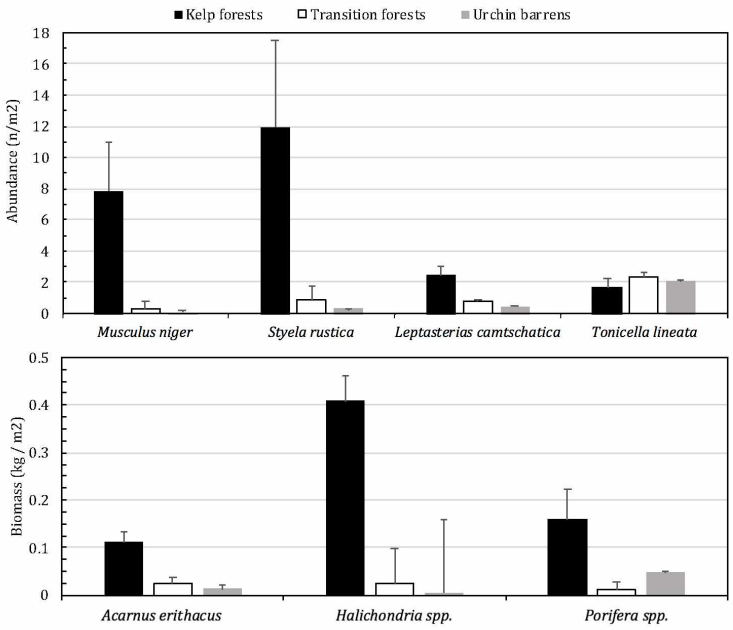

Figure 7: Bar charts of abundance (*top*) or biomass (*bottom*) data (± S.E.) from the seven taxa contributing most to the dissimilarity between habitats (Table 3).

Table 6: RELATE results testing for correlation between different algae or algal guilds and the associated faunal community or urchin size-structure.

Data stream	Algal data (biomass)	R	p
Faunal Biomass	Full community	0.298	0.001
	Subcanopy algae	0.298	0.001
	Fleshy red algae	0.240	0.001
	Eualaria fistulosa	1.888	0.23
	Laminaria spp.	0.298	0.001
	Agarum spp..	0.09	0.23
Sea urchin size frequency	Eualaria fistulosa	0.387	0.003
	Subcanopy algae	0.184	0.014
	Full community	0.184	0.0112

The final metric of community structure, percent cover, again showed a difference among habitats (PERMANOVA global test, Pseudo-F=4.766, $P_{(perm)}<0.001$, SS=12.089). Kelp forests exhibited significant differences from both transition forests and urchin barrens (T=2.140, $P_{(perm)}=0.004$; T=2.535, $P_{(perm)}=0.002$); however, transition forests and urchin barrens did not differ in their percent covers (T=1.012, $P_{(perm)}=0.420$) (Table 4; Figure 8). Higher percent cover of suspension feeders in kelp forests than in either transition forests or urchin barrens ($\bar{x} \pm S.E.$ = 26.652 ± 4.021%, 11.007 ± 2.616%, and 8.075 ± 1.810%, respectively) and lower cover of *Codium* spp. ($\bar{x} \pm S.E.$ =1.528 ± 0.422%, 2.291 ± 0.781%, and 2.472 ± 1.148%) were most responsible for driving dissimilarity between kelp forests and transition forests (suspension feeders=20.84% and *Codium* spp.=18.30%) and between kelp forests and urchin barrens (suspension feeders=20.79% and *Codium* spp.=18.02% (Table 5, Figure 8). Additionally, transition forests had higher cover of encrusting coralline algae than kelp forests ($\bar{x} \pm S.E.$ =43.002 ± 4.753% and 28.858 ± 2.40% respectively) that contributed 16.11% to the dissimilarity in percent cover between those habitats. Urchin barrens had higher cover of *Clathromorphum* spp. than kelp forests ($\bar{x} \pm S.E.$ =34.411 ± 6.230% and 18.287 ± 2.64%, respectively), and this also drove 16.27% of the dissimilarity between those habitats (Table 5, Figure 8).

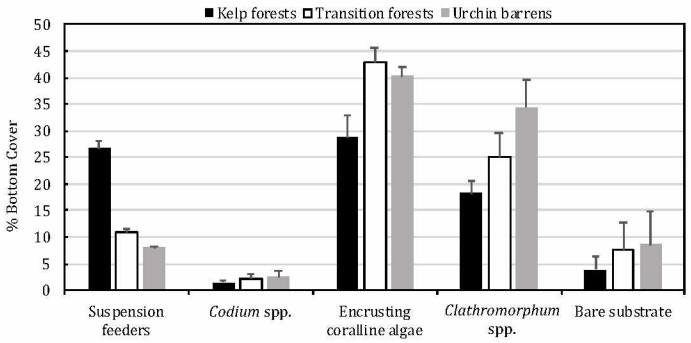

Figure 8: Bar chart of percent bottom cover (± S.E) by categories and among habitats. Suspension feeders and *Codium* spp. contributed most and second most to dissimilarity, respectively, between kelp forests and both transition forests and urchin barrens (Table 3).

3 Testing the hypothesis that habitats with more Eualaria biomass would have a higher proportion of large invertebrates.

Of the four taxa for which size frequency analyses were conducted, three (*Strongylocentrotus spp., Leptasterias camtschatica, and Lottia scutum)* showed significant differences among habitats, while *Henricia lineata* did not (Table 7). However, of those taxa shown to differ among habitats, *Leptasterias camtschatica* and *Lottia scutum* both exhibited

Table 7: ANOSIM results testing for difference in select invertebrate taxa's size frequency among habitats

Taxa	Habitats	R	p
Strongylocentrotus spp.	Kelp forests, transition forests	0.265	0.001
	Kelp forests, urchin barrens	0.282	0.001
	Transition forests, urchin barrens	0.016	0.186
Leptasterias camtschatica	Kelp forests, transition forests	0.015	0.165
	Kelp forests, urchin barrens	0.083	0.006
	Transition forests, urchin barrens	0.015	0.149
Lottia scutum	Kelp forests, transition forests	0.103	0.009
	Kelp forests, urchin barrens	0.163	0.013
	Transition forests, urchin barrens	0.034	0.183
Henricia lineata	Kelp forests, transition forests	-0.021	0.900
	Kelp forests, urchin barrens	-0.011	0.679
	Transition forests, urchin barrens	0.011	0.202

consistently low R-values <0.20, suggesting that habitat has little effect on these species' size frequency distributions (Table 7). Sea urchin (*Strongylocentrotus* spp.) size frequency distributions were significantly different in kelp forests than in both transition forests and urchin barrens; however, these differences did not exist between transition forests and urchin barrens (Table 7, Figure 9). While urchin abundance declined from urchin barrens to transition forests to kelp forests ($\bar{x}$ ± S.E.=156.11 ± 28.661 m^{-2}, 101.44 ± 16.941 m^{-2}, and 27.1 ± 6.36 m^{-2} respectively; Figure 4), the opposite pattern was seen for average test diameter ($\bar{x}$ ± S.D.=29.2 ± 14.6 mm, 33.1 ± 13.8 mm, and 36.8 ± 15.3 mm, respectively). This higher abundance of smaller sea urchins in urchin barrens resulted in a right-skewed size distribution, especially relative to the more symmetric distribution seen in kelp forests (Figure 9). Further, the majority of sea urchins over 80 mm were found in kelp forests, while sea urchins in those size classes were rare or absent in transition forests and urchin barrens (Figure 10). RELATE results show that sea urchin size structure, while significantly related to algal community structures from all guilds/guild combinations (*e.g., Eualaria's*, subcanopy, and full community), was most strongly correlated to *Eualaria's* biomass structure (Table 6).

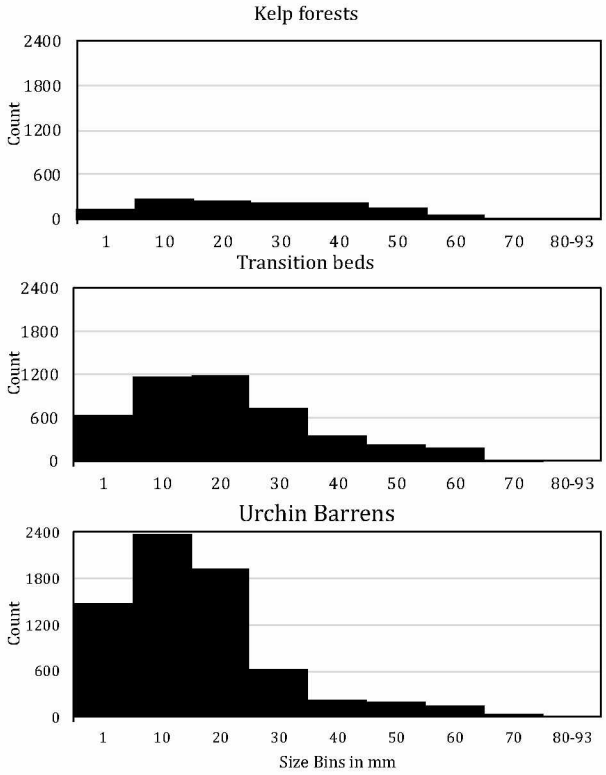

Figure 9: Size-frequency histograms of sea urchin populations (*Strongylocentrotus* spp.) among all sites and habitats.

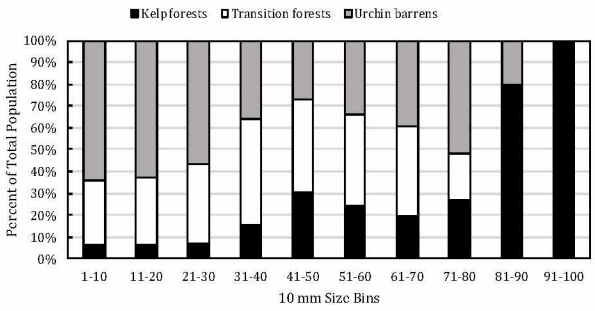

Figure 10: Stacked bar chart showing the percent contribution of sea urchins (*Strongylocentrotus spp.*; to 10 mm size bins) from each habitat, to the total population.

Discussion

Past studies evaluating kelp as foundation species have argued that certain kelps qualify as foundation species based on their productivity and provision of habitat, with little to no investigation into how the presence of those species influences the associated community structure (Mann 1973; Field et al. 1977; Drew 1983; Kirkman 1984; Larkum 1986; Graham et al. 2013). Other studies have investigated the effects on the associated community but have focused on a narrow subset of species (*e.g.*, suspension feeders; Eckman and Duggins 1991). This study sought to examine the entire epibenthic community to evaluate the ecological role of a purported foundation species, *Eualaria fistulosa*. Despite several suggestions that *Eualaria* acts as a foundation species (Estes and Palmisano 1974; Estes et al. 1978; Estes and Duggins 1995), this study's findings suggest that where *Eualaria* occurs as the sole dominant algal taxa, it does not act as a foundation species. No difference in community abundance, biomass, diversity, percent cover, or sea urchin size-structure were seen between transition forests (where the only fleshy algal cover is *Eualaria)* and urchin barrens. These results were supported by multivariate analysis results showing that subcanopy algal community structure is more strongly correlated with faunal community structure than is *Eualaria*. Indeed, by nearly every metric, transition barrens, where *Eualaria* is the sole dominant algal species were no different than urchin barrens where *Eualaria* was absent.

Given this study's region and design, it was neither possible to isolate the role of *Eualaria* from subcanopy nor conclude that the presence of *Eualaria* in kelp forests has no effect on community structure. It may well be that in kelp forests, *Eualaria* is working in tandem with other algal species, additively or even synergistically, and that this precipitates significant changes to the associated community. In fact, most ecosystems are structured by multiple foundation species, whose structural and morphological differences lead to unique influences to the associated community (Bruno and Bertness 2001; Ellison et al. 2005). Further, positive interactions among foundation species can result in facilitation cascades, where one or more primary habitat-formers facilitates secondary habitat-formers, and so on (Gribben et al. 2017). This facilitation cascade may well have been the case in the Aleutian nearshore before otter population declines resulted in

increased urchin grazing that removed subcanopy algae even where *Eualaria* persists, thus interrupting a facilitation cascade for which *Eualaria* was the basal foundation species.

Habitat fragmentation offers another potential explanation why isolated *Eualaria* do not play a foundational role. Habitat fragmentation is defined as a landscape process involving habitat loss, reduced patch size, and reduced patch density (Andren 1994). This definition closely matches the large-scale decline of this species in the Aleutians (Estes et al. 1998) and the resulting patchwork of kelp forests (Konar 2000b; Konar et al. 2014). Many early studies that investigated the impact of sea otter loss on the region's nearshore communities (Estes and Palmisano 1974; Estes et al. 1978) took place before the 1990s widespread collapse of sea otters (Doroff et al. 2003). At the time of these studies (1970-1973), sea otters were abundant and near equilibrium density at some islands, and absent at others (Estes and Palmisano 1974; Estes et al. 1978). Consequently, where sea otters were present "*benthic macrophytes...extend[ed] from the intertidal region and cover[ed] most of the surface of the rock substrate to depths of 20 to 25 m*" (Estes and Palmisano 1974). This observation stands in stark contrast to the distribution of kelp forests in the central and western Aleutians today. For this study, targeted searches for kelp forests had to be made, and many kelp forests were relatively small and restricted to rocky pinnacles or other high-relief features (Konar 2000a) more resilient to urchin induced deforestation (Konar 2000b). This fragmentation of kelp forest habitats likely has important ramifications for community structure and function; however, studies on fragmentation in the marine environment are few and largely focused on seagrass habitats (Eggleston et al. 1998; Hovel and Lipcius 2001; Hovel and Lipcius 2002). These studies have shown that habitat patch size can influence local community structure by shaping patterns of faunal recruitment and survival (Eggleston et al. 1998; Hovel and Lipcius 2001), but also emphasize that effects are species, density, and body-size dependent (Eggleston et al. 1998). Kelp patch size has also been seen to affect the associated community's structure (Bender et al. 1998) and can be positively correlated with fish abundances and biomass densities (Deza and Anderson 2010). Additionally, edge effects can drive community change in fragmented landscapes (Laurance et al. 2007). Edge effects are defined as physical and biotic alterations associated with boundaries of habitat fragments, and populations in fragmented habitats are increasingly exposed to ecological changes

associated with edges. For example, in a high-latitude kelp forest system, significantly different fish assemblages were found at kelp forests edges relative to the interior (Efird and Konar 2014). Edge effects in fragmented habitats are remarkably diverse, including: proliferation of shade-intolerant plants, change in microclimates and light regimes, increased exposure of fragmented habitats to generalist predators, and increased shear forces that can cause increased dislodgement and mortality (reviewed in Laurance and Yensen 1991). This last edge effect may be of particular importance. As many remnant Aleutian kelp forests are now restricted to areas with higher wave action and current flow such as pinnacles or boulder tops (personal observation; Konar 2000b), they may be subjected to higher shear forces increasing kelp dislodgment and reducing kelps' ability to modify hydrodynamic forces within kelp forests boundaries.

Another reason why isolated *Eualaria* may not function as a foundation species may stem from these forests current distribution being restricted to high-relief habitats. During the past two decades Aleutian sea otters appear to have shifted from foraging in low relief locations with few or no pinnacles to currently utilizing structurally complex, highly rugose areas of coastline (Stewart et al. 2014). A similar pattern appears to exist with remnant Aleutian kelp forest populations, where areas dominated by urchin barrens may have remnant, isolated kelp stands on isolated rocky pinnacles (Konar 2000b). This comparison does not suggest that remnant Aleutian otter populations are structuring remnant kelp populations (although where sea otters remain abundant this is likely the case). Rather, both sea otters and kelp are now restricted in their distributions to highly rugose areas due to a similar mechanism: reduced consumer access these areas (Konar 2000b; Stewart et al. 2014). As a canopy kelp, *Eualaria* can create extensive three-dimensional habitat for other species. However foundation species typically provide habitat on a scale that is disproportionate to the habitat provided by other species or (more pertinently) to the local physical structure (Graham et al. 2013). As kelp forests are now more restricted to high-relief structures, *Eualaria's* provision of complex three-dimensional habitat may no longer provide physical structure "disproportionate" to that of the highly rugose seafloors to which it is restricted thus, diminishing its role as a foundation species.

Other explanations for the observed community shift between kelp forests and transition forests may involve the communities themselves, namely, the abundance,

morphology, and community contribution of taxa therein. Subcanopy algae contributed substantially more algal biomass at kelp forests sites than the canopy kelp *Eualaria*. Additionally, subcanopy kelps can weaken fluid transport and increase particle deposition rates near the bottom. This has been shown to increase survivorship and growth of suspension-feeders (Eckman et al. 1989), a group shown in this study to be strongly affected by the shift from kelp forests to other habitats. Thus, the loss of subcanopy algae may not only remove a significant carbon source, but also reduce the deposition of other suspended material in addition to algal derived carbon. Additionally, the canopy kelp *Eualaria* has morphological characteristics that may lessen the amount of energy it provisions to the associated community. *Eualaria* has a central midrib, full of gas filled chambers that hold the blade in the water column (O'Clair and Lindstrom 2000), thereby suspending a high portion of biomass further away the substrate and potential consumers. *Eualaria* is also an annual species (O'Clair and Lindstrom 2000) that is often dislodged in masse during fall and winter storms, creating large, floating detrital mats that can travel hundreds of kilometers in areas with strong unidirectional currents (Krumhansl and Scheibling 2012). Unidirectional currents characterize the portion of the Aleutian Archipelago detailed in this study. The Alaska Costal Current and Alaska Stream flow westward along the south side of the archipelago, while the Aleutian North Slope Current flows eastward along the archipelago's north side (Hunt and Stabeno 2005). Furthering potential for algal rafts to remove organic material from the Aleutian nearshore is that raft dispersal is greatest in waters below 15°C due to decreased microbial degradation (Rothäusler et al. 2009). Typical Aleutian summertime temperatures are 5–10°C with winter temperatures around 0°C (Rodionov et al. 2005).

Sea urchins may also be shaping communities in ways other than consuming algae. Sea urchin grazing may structure faunal communities by causing a physical disturbance that likely negatively affects sessile invertebrates attached to the rocky substrate (Graham 2004). However, it is notable that sea urchins occurred among all habitats, and that kelp forests maintain full algal communities with urchin's present. Kelp forest communities supply large amounts of drift algal detritus and sea urchins in kelp forests or adjacent habitats may be fully satiated by these allochthonous inputs, eliminating their need to actively forage on attached plants (Harrold and Reed 1985; Scheibling and Hamm 1991).

When detritus is abundant, sea urchins can change their behavior from grazing on attached kelps to forming sedentary aggregations or hiding in cryptic habitats and relying on transported detritus (Harrold and Reed 1985; reviewed in Krumhansl and Scheibling 2012). However, tagged sea urchins on Shemya Island in the western Aleutians were seen to move between all habitats over a forty-eight-hour period in both summer and fall with urchin movement increasing in all habitat types during the fall as annual algal cover decreased (Konar 2000b). This increase in urchin mobility may be associated with food limitation, or, the urchin-algal interaction capable of maintaining kelp forest boundaries (Konar et al. 2014) may also deter direct urchin grazing within kelp forests when kelp densities are higher in summer. But as sea urchins in kelp forests generally have a higher gonad mass relative to total mass (an indicator greater fitness) than sea urchins in nearby barrens (Harrold and Reed 1985; Konar and Estes 2003), kelp forest sea urchins are likely not completely excluded from local food resources. Indeed, this study corroborated this, finding that sea urchins in kelp forest are on average larger with population size structures that differ from those areas with less algal biomass by having size-structures containing a higher proportion of large-sized individuals.

Aside from the impact to kelp forest communities themselves, the broad-scale habitat shifts and corresponding loss of a purported foundation species from much of the Aleutian Archipelago nearshore likely has other, large-scale ecosystem consequences. This study corroborated previous findings that, relative to nearby kelp forests, urchin barren have lower species richness (Graham 2004; Chenelot et al. 2011; Krumhansl and Scheibling 2012) and that communities dominated by sea urchins generally have very little fleshy macroalgae (Filbee-Dexter and Scheibling 2014). Consequently, urchin barrens tend to be significantly less productive (Miller et al. 2011), biodiverse, and provide fewer ecosystem services (Smale et al. 2013b). There are implications of this habitat shift for the greater Aleutian food-web structure, with complex, indirect effects already seen in the marine (Vicknair and Estes 2012), intertidal (Irons et al. 2016), and terrestrial realms (Anthony et al. 2008) Additionally, there are likely consequences for energy transport to nearby ecosystems (Duggins et al. 1989) and carbon cycling (Wilmers et al. 2012).

Energy transport, carbon cycling, and other ecosystem processes may be especially impacted due to one of the more striking community differences seen in this study: the

dramatic reduction of filter feeders outside of kelp forests. Of the seven taxa identified in SIMPER analyses as contributing most to dissimilarity between kelp forests and the other two habitats' communities, five taxa (*Musculus niger, Styela rustica, Halichondria* sp., *Acarnus erithacus,* and *Porifera* spp.) were filter feeders (Table 5). These taxa were more abundant and/or had greater biomass in kelp forests and had biomass declines of at least 70.4%, with an average decline of 90.6% outside of kelp forests (Figure 7). Additionally, suspension feeders were identified as the percent cover category contributing most to dissimilarity among habitats (Table 5), declining an average cover of 26.7% in kelp forests to 11.0% in transition beds and 8.1% in kelp forests (Figure 8). While filter feeding taxa represent disparate phyla with different filtration characteristics (Stuart and Klumpp 1984), collectively they can play a pivotal role in communities (Gili and Coma 1998; Ostroumov 2005). Filter feeders have been shown to stabilize and regulate ecosystems by removing algae, bacteria and seston from water column, influencing primary and secondary production in littoral food chains (Gili and Coma 1998). Additionally, filter feeders package their waste as fecal pellets, which can create a stable supply of organic material to the surrounding benthos where it becomes available for other consumers (Ostroumov 2005). Filter feeders are also important in systems as they can create complex, three-dimensional habitat, adding to communities' habitat heterogeneity and directly providing food for predators (Ostroumov 2005). The reason for the large decline of filter feeders outside of kelp forests is unknown but the lack of subcanopy kelps outside of kelp forests offers one explanation. Areas under subcanopy kelps have been shown to have slower water transport and increased particulate deposition (Eckman et al. 1989), which can significantly alter the growth, reproduction, and recruitment of benthic organisms including filter feeders (Eckman et al. 1989). Additionally, the presence of kelp detritus can greatly increase the growth rates of Aleutian benthic suspension feeders (Duggins et al. 1989). These factors combined may allow for greater recruitment and growth of filter feeders in Aleutian kelp forests, allowing them to outpace losses from mortality that may come from multiple sources, including predation. There are several species of Aleutian sea stars (Jewett et al. 2012) and nudibranchs (McDonald and Nybakken 1980) that prey on sponges. In addition, while sea urchins have strong algal preferences, *S. droebachiensis* consumes a wide variety of prey, including filter feeders, especially when algae are absent

as a food option (Himmelman and Steele 1971). Further, consuming invertebrate fauna with kelp has increased the gonadal growth of sea urchins (Knip and Scheibling 2007), growth that occurs after somatic growth requirements have been met (Minor and Scheibling 1997). Therefore, the increase in sea urchins in transition beds and urchin barrens might explain the lack of suspension feeders in those habitats, as well as the smaller maximum sizes of sea urchins in those habitats. It may also be that the presence of filter feeders in kelp forests is able to remove microscopic sea urchin larvae from the water column, preventing urchin recruitment into kelp forests and creating a feedback loop whereby urchin grazing on suspension feeders allows for more sea urchins, which in turn can further graze suspension feeders.

The findings of this study have implications for conservation and management of the Aleutian Island ecosystem. Aleutian sea otters have declined (Doroff et al. 2003) to the point where the southwestern Alaska stock have threatened status under the U.S. Endangered Species Act (70 FR 46366, 8 September 2005). This decline has resulted in the shift of Aleutian, nearshore rocky reefs from kelp forest to urchin barren dominated. Additionally, this shift has, and continues to have, many indirect effects impacting many different components of the Aleutian food web (Anthony et al. 2008; Vicknair and Estes 2012; Irons et al. 2016). Under the Endangered Species Act, the ultimate goal of recovery plans is to restore species to "ecological health" (U.S. Fish and Wildlife Service. 2013). Given the paradigm that where sea otters occur in sufficient densities, nearshore communities are kelp forest dominated (Estes and Palmisano 1974), recovery criteria have been adopted by the U.S. Fish and Wild Service that, "greater that 50% of the islands are in a kelp dominated state" (U.S. Fish and Wildlife Service 2013). With the remote nature and high cost of field studies in the Aleutian Islands, remote sensing of kelp coverage using satellite imagery (Jensen et al. 1980; Cavanaugh et al. 2010) is a promising, low cost avenue for monitoring this recovery criteria. However, this study found that kelp forests and transitional forests (both with intact *Eualaria* canopies visible using satellite imagery) differ in their communities. This reduces the applicability of remote sensing in this region or, at least, argues the need for some level of ground-truthing to determine the relative proportion of these habitats. Additionally, as transitional forests did not differ in their communities from urchin barrens, this study stresses caution in assuming transitional kelp

forests confer the same ecosystem services as intact kelp forests, such as elevated secondary production, nutrient cycling, energy capture and flow, costal defense, direct applications, and biodiversity repositories (Smale et al. 2013a).

Overall, this study contributes to a growing body of research that aims to assess the benefits that foundation species can confer to the associated community in terms of structure and biodiversity (Reisewitz et al. 2006; Watson and Estes 2011; Efird and Konar 2014; Schuster and Konar 2014). The results of this study reinforce the context dependence of foundation species where species may lose their ability to significantly alter communities in which they occur with changes to the system. Also, this study revealed that faunal community structure was significantly correlated with many algal species and algal guilds. Therefore, while the clearest application of the foundation species concept is to apply it to single species, in many contexts it may be more appropriate to identify "foundation guilds" to better advance scientific understanding of systems and facilitate management. Whether the diminished role of *Eualaria* is due to urchin grazing having interrupted a facilitation cascade, *Eualaria's* restriction to high-relief substrates, a previous overestimation of *Eualaria's* detritus contribution to communities, the physical impact of urchin grazing itself, or some other factor remains to be seen. But, these lines of investigation offer further avenues to better our understanding of the role of *Eualaria* in communities, and the functioning of foundation species in general. Learning how foundation species' influence on the associated community can fluctuate, both in the context of their populations and the context of the system in which they exist, is vital to furthering our understanding of their role in ecosystems.

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Appendices

1 IACUC Approval letters

2016 IACUC protocol approval

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Institutional Animal Care and Use Committee

909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

May 17, 2016

To:	Brenda Konar, PhD Principal Investigator
From:	University of Alaska Fairbanks IACUC
Re:	[899401-2] Aleutian Kelp Forest

The IACUC reviewed and approved the Amendment/Modification to the Personnel List referenced above by Administrative Review.

Received:	May 9, 2016
Approval Date:	May 17, 2016
Initial Approval Date:	May 5, 2016
Expiration Date:	May 5, 2017

This action is included on the June 9, 2016 IACUC Agenda.

PI responsibilities:

- *Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.*
- *Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)*
- *Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.*
- *Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.*
- *Ensure animal research personnel are aware of the reporting procedures on the following page.*

2017 IACUC protocol renewal

UNIVERSITY OF ALASKA FAIRBANKS

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Institutional Animal Care and Use Committee

909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

June 14, 2017

To:	Brenda Konar, PhD Principal Investigator
From:	University of Alaska Fairbanks IACUC
Re:	[899401-3] Aleutian Kelp Forest

The IACUC has reviewed the Progress Report by Designated Member Review and the Protocol has been approved for an additional year.

Received:	June 12, 2017
Initial Approval Date:	May 5, 2016
Effective Date:	June 14, 2017
Expiration Date:	May 5, 2018

This action is included on the July 13, 2017 IACUC Agenda.

PI responsibilities:

Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.

Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)

Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.

Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.

Ensure animal research personnel are aware of the reporting procedures detailed in the form 005 "Reporting Concerns".

2 *Alaska Dept. Fish and Game Collection Permits*

2016 Fish Resource Permit CF-16-086

STATE OF ALASKA
DEPARTMENT OF FISH AND GAME
P.O. Box 115526
JUNEAU, ALASKA 99811-5526

Permit No. **CF-16-086**

Expires: **7/31/2016**

FISH RESOURCE PERMIT
(For Scientific/Collection/Holding Purposes)

This permit authorizes: **Jacob Metzger**
(whose signature is required on page 2 for permit validation)
of
University of Alaska Fairbanks
P.O. Box 757220, Fairbanks, AK 99775
(907)738-9907 jrmetzger@alaska.edu

to conduct the following activities from **June 1, 2016** to **July 31, 2016** in accordance with AS 16.05.930 and AS 16.05.340(b).

Purpose: To study how the loss of kelp forests impact onshore and offshore benthic diversity and benthic primary production. Photosynthesis and respiration rates of kelp and urchins will be monitored insitu and onboard.

Location: For Islands Tanaga, Adak, Atka, Chuginadak, and Seguam – 6 SCUBA and 1 trawl site per island
For Islands Anagula, Unalaska, and Akutan – Opportunistic sampling not to exceed 6 SCUBA and 1 trawl site per island

Species: See **Species List** on page 3.

Method of Collection: Hand collection via scuba, and plumbstaff beam trawl.

Disposition: Species will be sacrificed as voucher specimens. Some kelp and urchins will be held live onboard the *R/V Oceanus* for monitoring and sacrificed at the end of the project. See **Stipulations** section.

A COLLECTION REPORT IS DUE August 30, 2016 and a **COMPLETION REPORT IS DUE January 30, 2017**. See **Stipulations** section for more information. Data from such reports are considered public information. Reports must be submitted to the Alaska Department of Fish and Game, Division of Commercial Fisheries, PO Box 115526, Juneau, AK 99811-5526, attention Michelle Morris (907-465-4724; dfg.fmpd.permitcoordinator@alaska.gov). A report is required whether or not collecting activities were undertaken.

GENERAL CONDITIONS, EXCEPTIONS AND RESTRICTIONS

1. This permit must be carried by person(s) specified during approved activities who shall show it on request to persons authorized to enforce Alaska's fish and game laws. This permit is nontransferable and will be revoked or renewal denied by the Commissioner of Fish and Game if the permittee violates any of its conditions, exceptions or restrictions. No redelegation of authority may be allowed under this permit unless specifically noted.
2. This permit is for non-propagative research that requires maintaining live specimens for some amount of time after capture.
3. No specimens taken under authority hereof may be sold, bartered, or consumed. All specimens must be deposited in a public museum or a public scientific or educational institution unless otherwise stated herein. Subpermittees shall not retain possession of live animals or other specimens.
4. The permittee shall keep records of all activities conducted under authority of this permit, available for inspection at all reasonable hours upon request of any authorized state enforcement officer.
5. Permits will not be renewed until detailed reports, as specified in the Stipulation section, have been received by the department.
6. UNLESS SPECIFICALLY STATED HEREIN, THIS PERMIT DOES NOT AUTHORIZE the exportation of specimens or the taking of specimens in areas otherwise closed to hunting and fishing; without appropriate licenses required by state regulations; during closed seasons; or in any manner, by any means, at any time not permitted by those regulations.

Peter Bangs 4/22/16
Deputy or Assistant Director
Division of Commercial Fisheries
Alaska Department of Fish and Game

STATE OF ALASKA
DEPARTMENT OF FISH AND GAME
P.O. Box 115526
JUNEAU, ALASKA 99811-5526

Permit No. **CF-17-096**

Expires: **7/31/2017**

FISH RESOURCE PERMIT
(For Scientific/Collection/Holding Purposes)

This permit authorizes: **Jacob Metzger**
(whose signature is required on page 2 for permit validation)
of
University of Alaska Fairbanks
P.O. Box 757220, Fairbanks, AK 99775
(907)738-9907 jrmetzger@alaska.edu

to conduct the following activities from **July 1, 2017** to **July 31, 2017** in accordance with AS 16.05.930 and AS 16.05.340(b).

Purpose: To study how the loss of kelp forests impact onshore and offshore benthic diversity and benthic primary production. Photosynthesis and respiration rates of kelp and urchins will be monitored insitu and onboard.

Location: For islands Attu, Aggattu, Shemya, Hawadax (Rat), Amchitka, Tanaga, – 6 SCUBA and 1 trawl site per island
For islands Kiska, Ogliuga, Adak, Yunaska – Opportunistic sampling not to exceed 6 SCUBA and 1 trawl site per island

Species: See **Species List** on pages 3-4.

Method of Collection: Hand collection via scuba, plumbstaff beam trawl, pole-spear, hook-and-line.

Disposition: SCUBA and trawl collected species will be either 1) identified, measured, and released or 2) identified, measured, held alive for up to 24hr respiration incubations, then released.
Fish species taken by pole-spear or hook-and-line will be sacrificed, tissue samples taken, then disposed of. Up to 2 individuals from unknown species may be sacrificed, suspended in formalin, and saved for later identification. See **Stipulations** section.

A COLLECTION REPORT IS DUE August 30, 2017 and a **COMPLETION REPORT IS DUE January 30, 2018**. See **Stipulations** section for more information. Data from such reports are considered public information. Reports must be submitted to the Alaska Department of Fish and Game, Division of Commercial Fisheries, PO Box 115526, Juneau, AK 99811-5526, attention Michelle Morris (907-465-4724; dfg.fmpd.permitcoordinator@alaska.gov). A report is required whether or not collecting activities were undertaken.

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Peter Bangs 6/16/17
Deputy or Assistant Director
Division of Commercial Fisheries
Alaska Department of Fish and Game